

RELATIONSHIPS OF TWO ISOLATED GROUPS OF SUGAR
MAPLES (*ACER SACCHARUM* MARSHALL
SSP. *SACCHARUM*) IN WEST CENTRAL OKLAHOMA
TO EASTERN AND WESTERN SPECIES

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ABSTRACT

Two groups of sugar maples in west central Oklahoma which have been described as relicts were compared by numerical methods to eastern and western U.S. references. The populations of the Wichita Mountains, Comanche Co. have previously been assigned to the equivalent of *Acer saccharum* Marshall subsp. *grandidentatum* (Torrey and Gray) Desmarais (sensu lato) by some authorities and to *Acer saccharum* Marshall subsp. *saccharum* by others. Those of the Caddo Canyons, Caddo and Canadian counties have been consistently designated as *Acer saccharum* Marshall subsp. *saccharum*. The two groups have a north-south separation of ca. 80 km. The continuous range of *A. s.* subsp. *saccharum* penetrates eastern Oklahoma as an irregular fringe ca. 320 km east of the prairie groups. The closest stations for subsp. *A. s. grandidentatum* are ca. 480 km west of the Oklahoma locations in the Monzano Mountains of New Mexico and ca. 680 km southwest in the Edwards Plateau of Texas.

A principal coordinates analysis of micromeasurements of leaf samples from 160 populations collected in the four major geographic areas (eastern and western U.S. and Caddo Canyons and Wichita Mountains of Oklahoma) supports the hypothesis that the best designation for both Oklahoma groups is *A. s.* subsp. *saccharum*. These results indicate that single organs of some plants exhibit a high degree of reliability when extensive micromeasurements are used to detect genetic affinities.

KEY WORDS: Sugar Maple, *Acer saccharum*, Oklahoma, Numerical Taxonomy, Principal Coordinates, Relicts

Two isolated groups of sugar maples (*Acer saccharum* Marshall subsp. *saccharum*) occur in the prairies of west central Oklahoma approximately 320 km west of the edge of the continuous range of the eastern representatives of the species (Fig. 1). The nearest western relatives of these plants (*Acer saccharum* Marshall subsp. *grandidentatum* (Torrey and Gray) Desmarais (sensu lato)) occur ca. 480 km west in the Monzano Mountains of New Mexico and ca. 680 km southwest in the Edwards Plateau of Texas. The isolated Oklahoma populations are found in protected places in most of the canyons of the Caddo Canyons, Caddo and Canadian Counties, and approximately 80 km south in similar habitats in deep, sheltered canyons

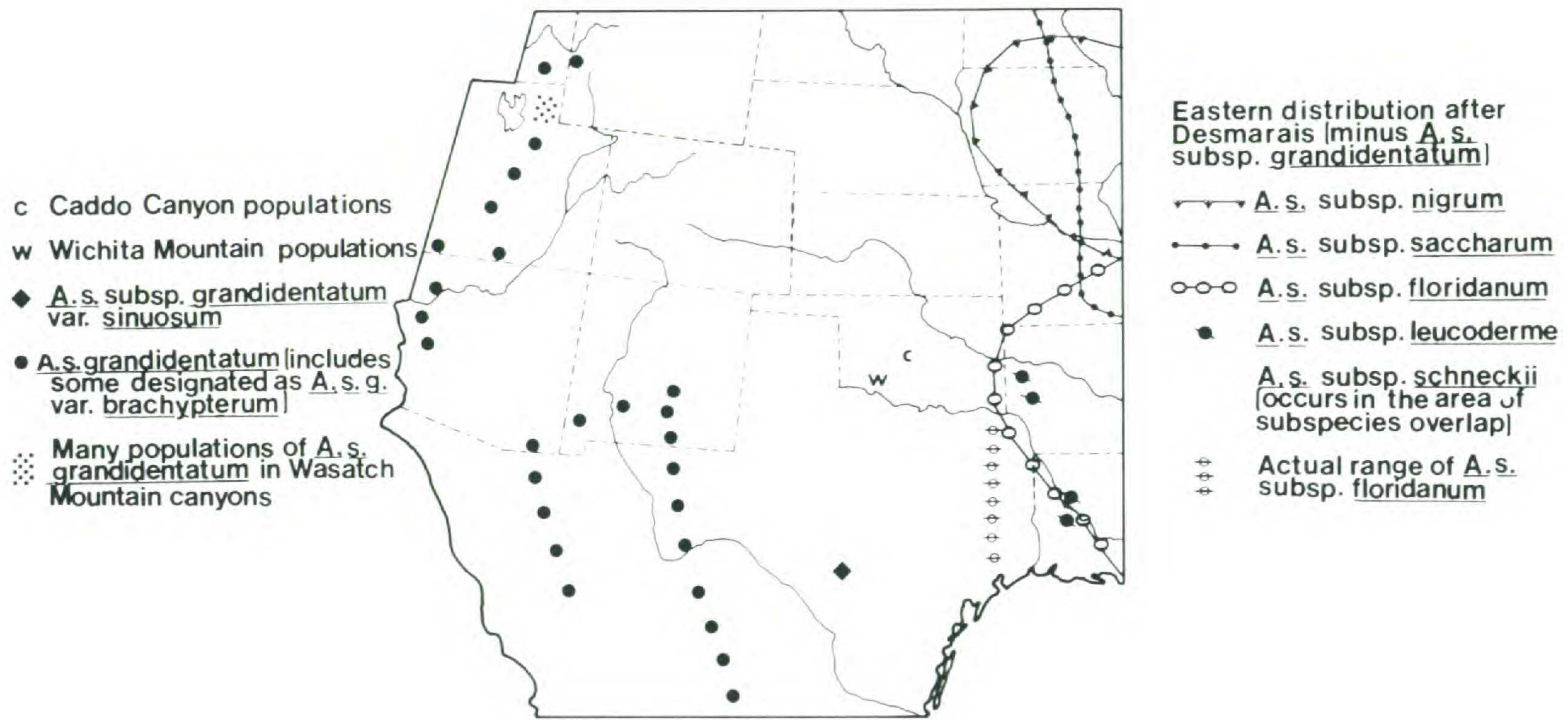


Fig. 1. Distribution of sugar maple within which study sampling areas are located. Eastern ranges are after Desmarais (1952) except as noted. Oklahoma, western and Mexican locations are from population samples and herbarium records.

and north facing draws of the Wichita Mountains of Comanche County.

The Caddo Canyon plants have always been designated as subsp. *saccharum*. The populations of the Wichita Mountains were first assigned to *A. grandidentatum* Nuttall by Sargent (1922) with citation from an unpublished thesis by Stevens (1916). This represented a change from his inclusion of these plants as *A. saccharum* Marshall in the earlier 1905 edition of the Manual of Trees of North America. This idea of the more southern Oklahoma plants having western affinities was supported by Palmer (1934) who based his decision on the close field similarity of the plants of the Wichita stations to those in western locations. Little (1939, 1944) reinforced this interpretation. Hopkins (1943), however, recognized both groups as *A. saccharum*. He suggested that the plants of the Wichitas were ecological variants of the eastern species. Recent referrals agree with Hopkins' interpretation (Buck, 1964; Rice, 1960; Risser et al 1977), an exception being the work of Gehlbach and Gardner (1983).

The present investigation used a principal coordinates analysis of micromeasurements of leaf samples from 160 populations collected in the four major geographical areas involved; eastern and western United States and the Caddo Canyons and Wichita Mountains. This statistical procedure has resulted in a more objective conclusion about the relationship of the two groups to each other and their eastern and western relatives.

METHODS

Measurements were based on Anderson and Hubricht's (1938) average leaf technique (Fig. 2). Raw measurement data¹ from selected populations from those studies were used directly for part of the eastern reference group. A second set of populations was taken from samples which had been pooled with the Anderson and Hubricht materials from studies done by Dansereau and Lafond (1941), Dansereau and Desmarais (1947), and Desmarais (1952). Pubescence

¹See end of Appendix for availability of all raw measurement data for all populations included in this study.

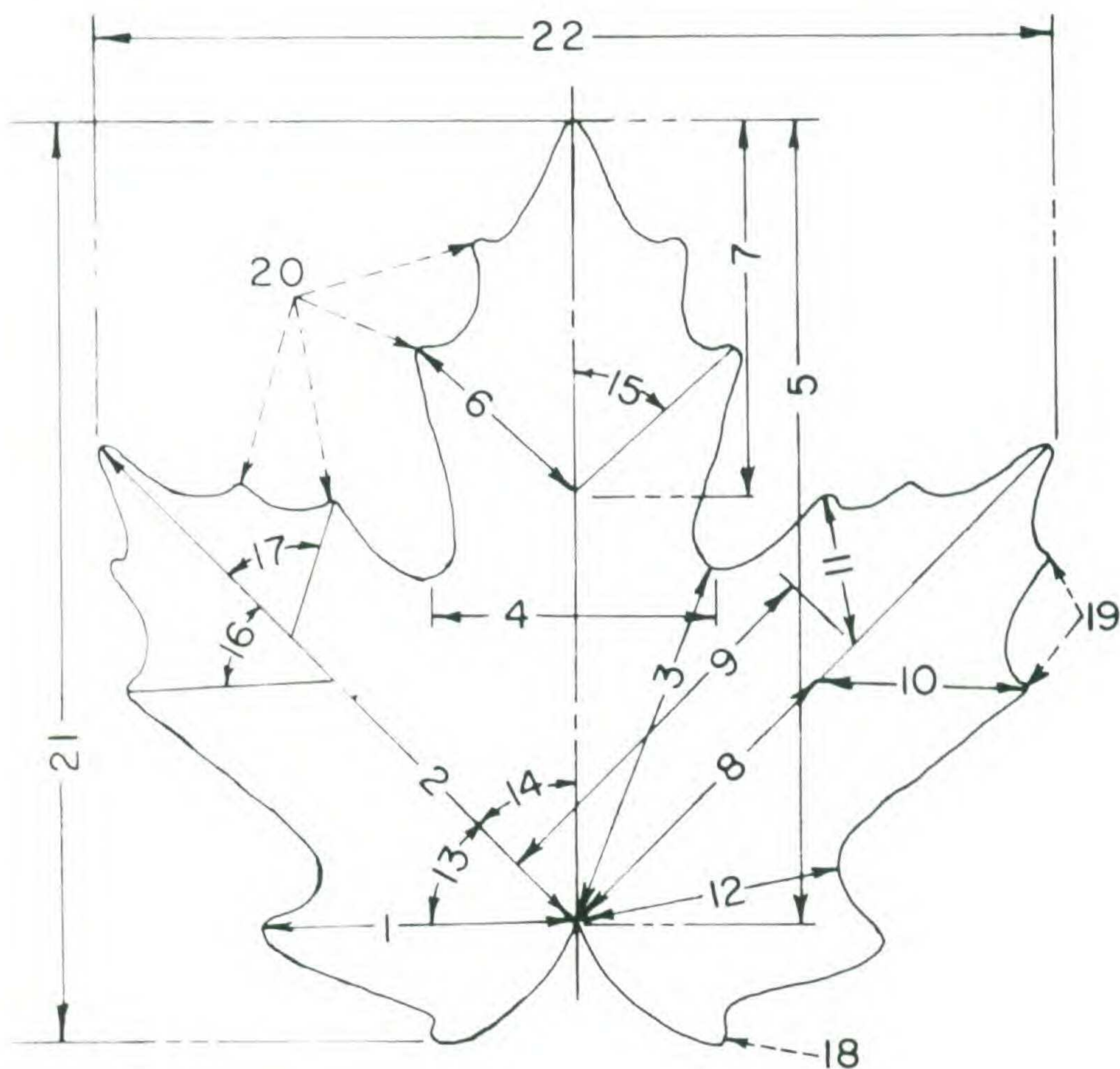


Fig. 2. Key to leaf measurements (Anderson and Hubricht, 1938).

scoring data were used directly from these studies but linear and angular measurements and lobe counts (1-22, Fig. 2) had to be taken because a subjective leaf shape coding technique had been substituted for these characters. These measurements, along with those for several new station additions, yielded an eastern reference of 50 populations (Appendix). Most of the populations used were selected from stations at the western edge of the range of the eastern groups so that they were located nearest to the Oklahoma isolates. They were for the most part those which Desmarais (1952) had coded as pure stands of *Acer saccharum* Marshall subsp. *saccharum*, subsp. *nigrum* (Michaux f.) Desmarais, subsp. *floridanum*

(Chapman) Desmarais, and subsp. *schneckii* (Rehder) Desmarais. Desmarais had only one small part of one collection designated as subsp. *leucoderme* (Small) Desmarais and no other populations were visited so this sole subspecies apparently was not represented in the numerical analysis of any study.

For populations from Oklahoma, southwestern United States, and an extensive western United States reference (Appendix), the sampling technique of Anderson and Hubricht (1938), which had also been employed by Desmarais et al, was utilized. Leaves were selected from 20 to 50 individuals but in some situations stand size restrictions yielded smaller representations. The population was inspected for a visual impression of a standard size and shape, majority leaf. One leaf was then subjectively chosen from each tree, from sterile stems, with at least two years growth and in semi-shade. An attempt was made to select the leaf at shoulder height where possible and atypical growth such as base sprouts, which often exhibit unusually large and sometimes shape distorted leaves, were avoided. Leaves were press dried, numbered, and stored in newspaper.

Pubescence density, undersurface color, and stipule presence scoring (characters 20–26, Table 1) was done for the new populations sampled for this study with a standard binocular microscope. The photographs from Desmarais (1952) were used as references. Figures 3 and 4 represent a clearer scanning electron microscope perspective for the pubescence judgments. A new pubescence character evaluating the density of indumentum along the edges of leaf margins was recorded for all populations included in the study (character 27, Table 1). The Demarais (1952) density criteria were used to score the marginal hair presence as pubescent, intermediate, or glabrous.

For the statistical analyses, linear measurements were converted to ratios (Fig. 2 and Table 1) to avoid the effect of ecomorphic distortion which would result if only gross leaf size was considered. A selected number of populations was used as individual operational taxonomic units (OTUs). In seven situations a number of populations was combined to form exemplar OTU blocks (Appendix 1).

Analysis of variance (ANOVA) was run for each of the 27 characters to obtain F ratios (Table 1) and weights for various combinations of populations. The similarity measure used was an F-1

Table 1. Characters, character state values and F-ratios used in the computation of similarity ratios. Weights are F-1.0, where F is from analysis of variance of seven reference sample sets: FL 1, floridanum 1 (159 leaves); FL 2, floridanum 2, (34); UT, Utah populations of grandidentatum (254); NIG, nigrum (111); SAC 1, saccharum 1 from border states (181); SAC 2, saccharum 2 from eastern U.S. (237); and SCH schneckii (197). $F_{.05} = 2.11$; $F_{.01} = 2.82$; $df = 6/1168$. See Fig. 2 for character definitions.

Character	Character State Value	F-Ratio
1. 5/2 ¹ ratio	actual value	13.2
2. 5/1 ratio	actual value	35.0
3. 5/7 ratio	actual value	18.0
4. 7/6 ratio	actual value	28.2
5. (2-9)/11 ratio	actual value	33.8
6. (2-8)/10 ratio	actual value	33.8
7. 22/21 ratio	actual value	33.9
8. 3/12 ratio	actual value	24.9
9. (2-3)/(5-3) ratio	actual value	20.1
10. (1-12)/(2-12) ratio	actual value	33.2
11. (sin. angle 15 × length 6)/ (.5 × length 4) ratio	actual value	13.0
12. angle 13	actual value	150.6
13. angle 14	actual value	39.9
14. angle 15	actual value	27.0
15. angle 16	actual value	83.2
16. angle 17	actual value	100.0
17. lobe count 18	actual value	80.0
18. lobe count 19	actual value	137.0
19. lobe count 20	actual value	189.3
20. petiole pubescence	(P) ² ,(I)1,(G)0	14.8
21. lower epidermis main vein pubescence	(P)2,(I)1,(G)0	266.2
22. lower epidermis general pubescence	(P)2,(I)1,(G)0	289.1
23. lower epidermis main axil	(P)2,(I)1,(G)0	197.2
24. pubescence type	(E)1,(I)2,(A)3,(O),0	227.6
25. lower epidermis color	(Y)1,(G)2,(V)0	266.7
26. stipule presence	(O)0,(S)1,(L)2	67.3
27. marginal hairs	(P)2,(I)1,(G)0	139.1

¹See Figure 2.

²Anderson and Hubricht (1938) designations: petiole, various lower epidermis, and marginal hair density (P=very pubescent, I=intermediate pubescence, G=glabrous); position of hairs relative to the lower epidermis (E=erect, A=appressed, I=intermediate, O=glabrous); color of lower epidermis (Y=yellow green, G=glaucous, V=green); nature of stipules (O=absent, S=stipules, L=leaf-like stipules). Also see Figures 3 and 4 for pubescence characteristics.

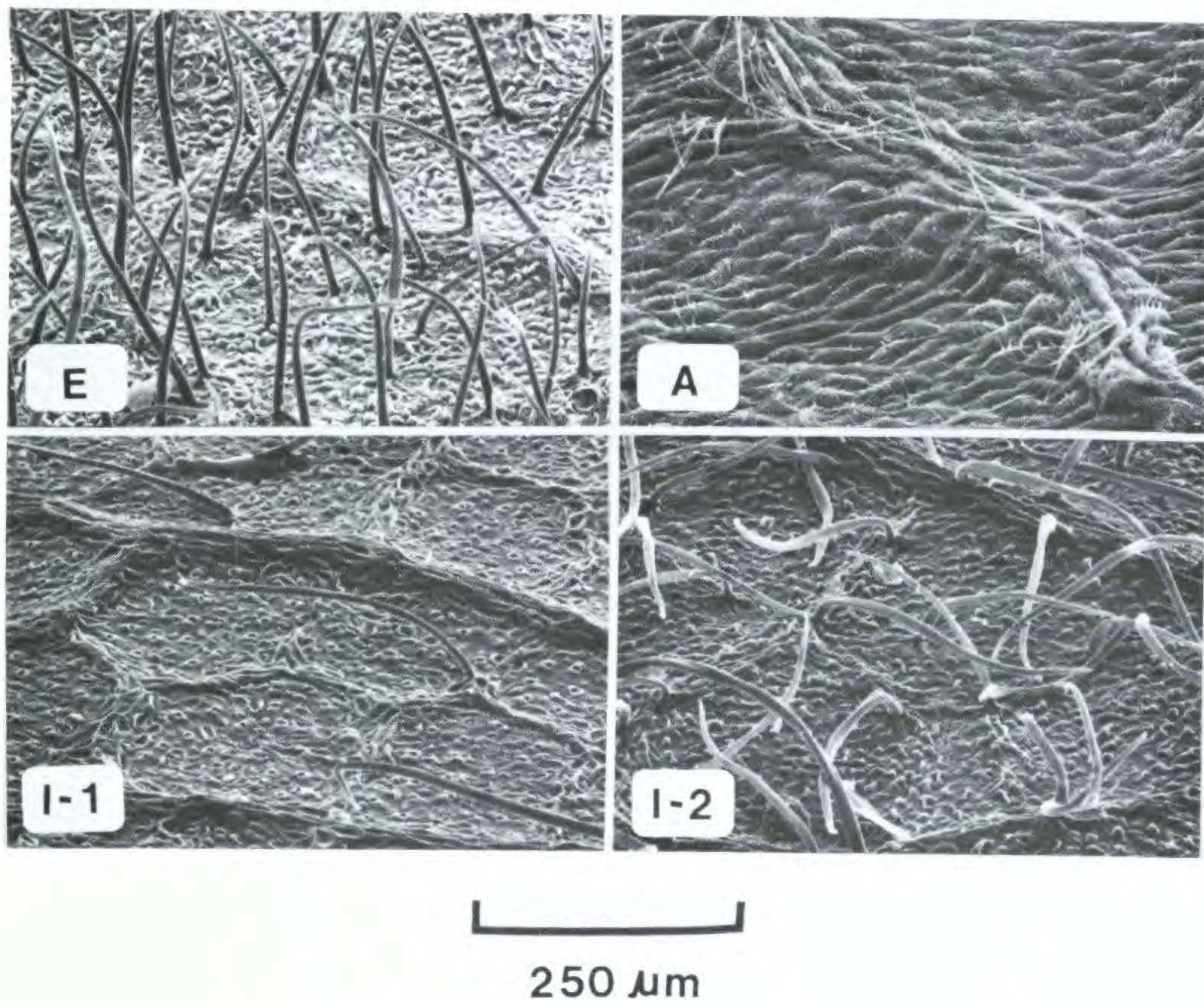


Fig. 3. Pubescence (see Table 1). Columns (density): P = very pubescent; I = intermediate pubescence; G = glabrous. Rows (character number): 20, petiole; 21, lower epidermis main vein; 22, general lower epidermis; 23, lower epidermis main axil; 27, marginal hairs.

weighted (F from ANOVA) mean character difference (MCD) as formulated by Adams (1975). Principal coordinate analyses (PCOORD) (Gower, 1966; Williams, Dale, and Lance, 1971) were performed using the similarity matrices for: 40 populations of *A. s.* subsp. *grandidentatum*; 18 populations of subsp. *saccharum* plus 6 populations of subsp. *nigrum*; and 20 populations of subsp. *floridanum* plus 14 populations of subsp. *schneckii*. From these PCOORD runs representative populations were chosen for use in constructing the exemplars. It should be noted that PCOORD of the *saccharum-nigrum* populations revealed three distinct clusters and accordingly subsp. *saccharum* was divided into two exemplars: SAC 1 and SAC 2. This was also the case for subsp. *floridanum* which was divided into FL 1 and FL 2. The population numbers included in the exemplars are shown in the Appendix. This generated a set of F ratios

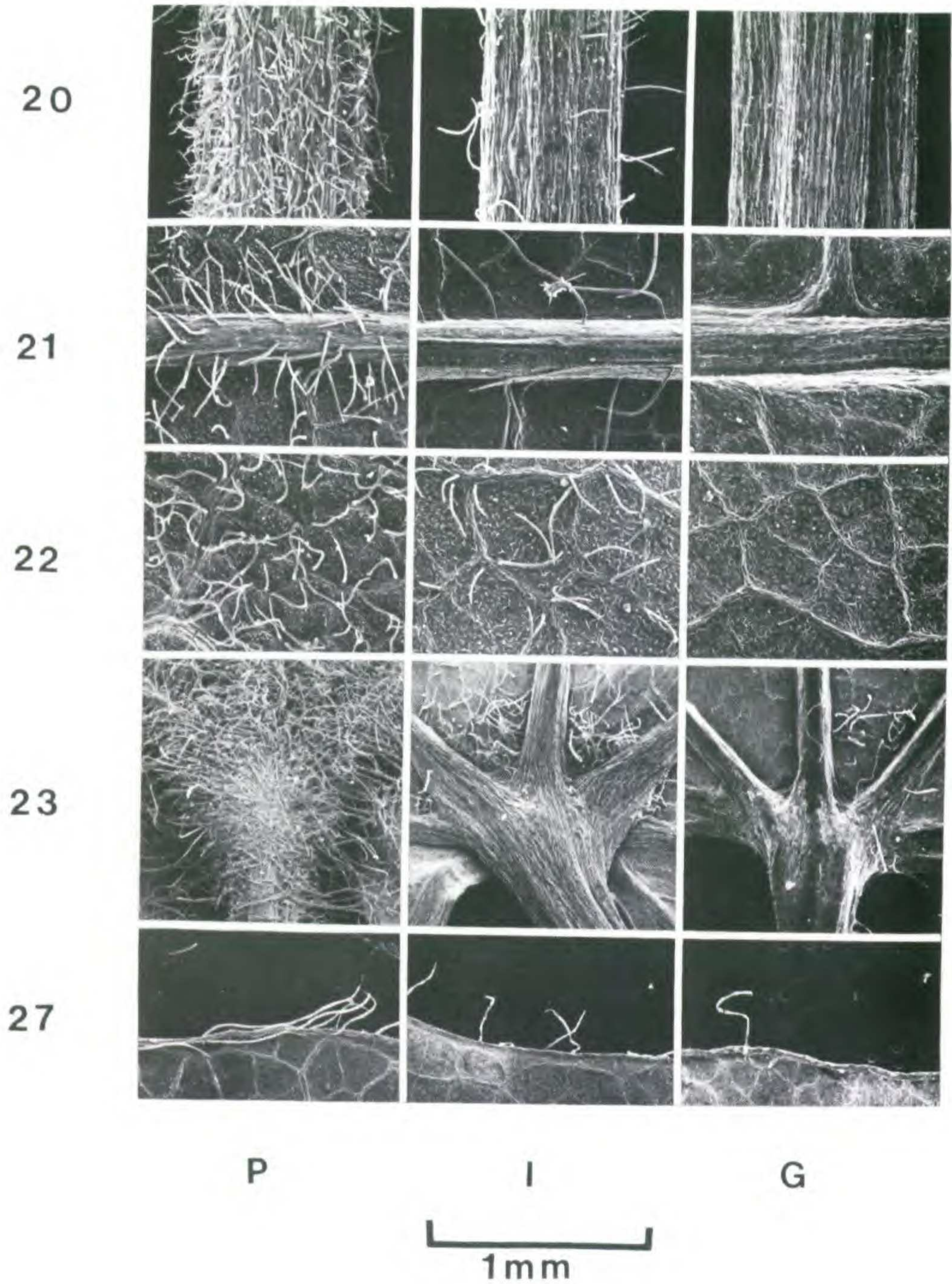


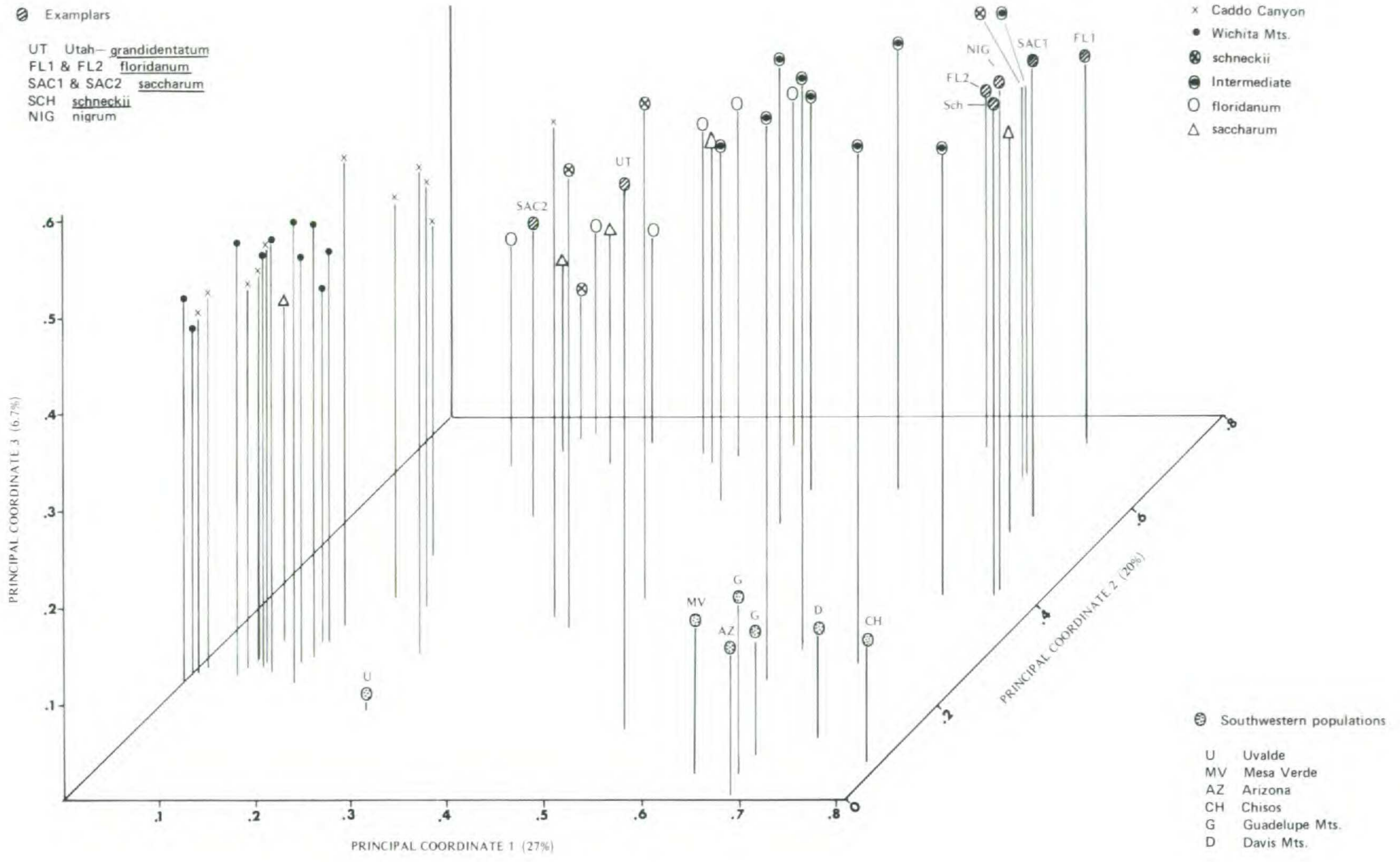
Fig. 4. Type of pubescence (see Table I, character 24). E = erect; A = appressed; I-1 = intermediate with most hairs in median position; I-2 = intermediate with approximately equal distribution of hairs in all positions.

(Table 1) which maximally discriminated between these seven exemplars, 12 Caddo populations, 10 Wichita populations, 7 southwestern United States populations, and 25 border state eastern populations by using weights from ANOVA of the seven exemplars. Principal coordinate analyses were then run on these 61 OTUs' similarity matrix to determine the affinities of the central Oklahoma populations to each other and to the western, southwestern and border state populations.

Six eigenroots were extracted (4.05, 2.92, 0.99, 0.82, 0.69, 0.52; Trace = 14.87) accounting for 67.3% of the variance. Each eigenroot explains a proportional amount of variation of the pattern among the OTUs. It is useful to represent these relationships in multidimensional space. Only the first three are presented here (Fig 5) as they appear to asymptote toward an error variance after the third root.

DISCUSSION

The ordination diagram of the first three principal coordinates (Fig. 5), reveals distinct separation of the four major geographical groups. The six southwestern populations (a fifth group) are also separated from the others. The western representatives (Exemplar UT) align distinctly with the southwestern groups in the plane of PCOORD 1 and 2 but exhibits an interesting projection along axis 3. The two Oklahoma groups are indicated as more similar to each other than either is to the eastern and western references. The diagram also reveals a spatial orientation of the Oklahoma groups toward the eastern samples, especially in the plane of principal coordinates 1 and 2. In fact, one population from the Caddo Canyons and one from Rich Mountain, Arkansas fall within the boundary of the other. These placements, along with the strong field resemblance of the Caddo plants to eastern groups, is more persuasive that the populations of both Oklahoma stations are more recently influenced by the eastern gene pool. The decidedly strong subjective impression of the similar field morphology of the Wichita plants to western species is also outweighed by this statistical evidence.



An earlier numerical analysis was made using the 80 populations referred to above from the east, 50 populations from the west and all of the samples from the Caddo Canyons and Wichita Mountains (Dent, 1969 a and b). A modification of the total difference index method of Russell (1964) was used. The results were similar to this current study but the more powerful PCOORD treatment presented here is considered more reliable.

The proposal of Little (1939, 1944) that the more southerly Wichita Mountain groups were more influenced by western subsp. *grandidentatum* germ plasm and the Caddo Canyon plants by eastern subsp. *saccharum* was not supported. This idea was originally presented based on subjectively perceived field similarities of the Wichita plants to western species (Palmer, 1934) and hypotheses of Sears (1932, 1933). Sears suggested that alternating mesic and xeric climates were induced in the interior plains by the irregular withdrawal of the Wisconsin ice sheet in the northern latitudes. Little's application proposed that the Oklahoma sugar maples represent arborescent survivor species of the two factions of a xerically separated but once continuous mid-continental east to the west distribution across the great plains. These flora were proposed to have approached within 80 km of each other during the last mesic (limited glacial advance) cycle. The southern vegetation tongue which terminated in the Wichita Mountains had developed western characteristics and the eastern derived fringe ended at the Caddo Canyons.

The final glacial retreat resulted in a return to a more xeric climate and the elimination of the more mesic-dependent species. The result over time was the establishment of the present, drier prairie flora. Sugar maple remained in more protected mesic sites as the only extant woody relict of this proposed migrational activity. All other species either persisted in a continuous range across the great plains (xeric tolerant) or were xerically terminated at the eastern edge of the prairies.

The mixture of eastern and western herbaceous flora found in both the Caddo Canyons and the Wichita Mountains indicated

Fig. 5. Principal coordinate analysis. Note how the Caddo and Wichita populations cluster and the affinity of these to eastern populations. See Appendix for specific populations indicated by the key above.

some support for this interpretation (Hopkins, 1938 and 1943; Little, 1939; Rice, 1960) but the argument for a recent common association with the retreating mesic eastern flora for both west central Oklahoma sugar maple groups is more compelling. A recent study (Gehlbach and Gardner, 1983) which combined a similar numerical analysis with a flavonoid compound assessment concludes the opposite in favor of the Little designations and in addition assigns the Caddo plants to the hybrid status *A. s.* subsp. *floridanum* × *grandidentatum*.

The clustering indicated by the PCOOR ordination diagram (Fig. 5) reveals good separations for the major geographically identified groups (eastern, western-southwestern and Oklahoma). It does not present a clear picture for the traditional subspecies designations applied within the eastern United States range.

CONCLUSIONS

The principal coordinate evidence generated by this study indicated that the sugar maples of the Caddo Canyons and the Wichita Mountains of west central Oklahoma, while significantly isolated from each other and their eastern and western United States relatives, are more similar to each other than to outside reference populations, but are both more firmly aligned with eastern relatives. The eastern affinity hypothesis for both groups was reinforced by the few of those Caddo populations and the single western Arkansas representative which stray from their primary concentrations in the direction of the other. The best designation for all of the Oklahoma populations including the west-central isolates, is indicated to be the contemporary usage *Acer saccharum* Marshall subsp. *saccharum*. Use of the microanatomy of the leaf of these plants was a reliable statistical discriminator for large population groups but did not support the traditional sub-species designations for eastern United States.

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APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS

POPULATION NO. ¹	STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
CADDO CANYONS (12 populations)					491
1	OK	Caddo	Red Rock Canyon	35	
2	OK	Caddo	Devil's Canyon, Pioneer Camp #2	34	
3	OK	Canadian	Devil's Canyon Widder Maker	44	
4	OK	Canadian	Devil's Canyon Methodist Campground	53	
11	OK	Caddo	Salyor Lake	57	
12	OK	Caddo	Wildcat Creek	57	
71	OK	Canadian	Upper Kickapoo Creek	26	
72	OK	Canadian	Kickapoo Valley	36	
73	OK	Caddo	Medicine Creek	36	
74	OK	Canadian	Water Canyon	44	
163	OK	Caddo	Red Rock State Park Main Canyon	27	
164	OK	Caddo	Devil's Canyon Pioneer Camp	42	
WICHITA MOUNTAINS (10 populations, Wichita Wildlife Refuge)					495
5	OK	Comanche	Hollis Canyon	60	
6	OK	Comanche	Mount Pinchot	53	
7	OK	Comanche	Baker Peak No. 1	60	
8	OK	Comanche	Baker Peak No. 2	40	
9	OK	Comanche	Panther Creek	42	
10	OK	Comanche	Greenleaf Canyon	41	
13	OK	Comanche	Boulder Camp	57	
77	OK	Comanche	Halley Canyon	42	
162	OK	Comanche	Mount Scott	40	
178	OK	Comanche	Elk Mountain	60	

¹Numbers assigned by Dent for new population samples and to those used from previous studies.

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO. ¹	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
TEXAS-SOUTHWEST (7 populations)					277
14	TX	Bandera	Vanderpool	42	
			Warren Murphy Ranch		
15	TX	Brewster	Big Bend N.P.	52	
			Boot Springs		
16	TX	Jeff Davis	Toyahville	45	
			Little Ajuga Canyon		
17	TX	Culberson	McKittrick Canyon	48	
20	CO	Montezuma	Mesa Verde	46	
130*	AZ	Cochise	Coronado N.F.	10	
			Oak Creek Canyon		
168	TX	Culberson	Pine Springs	34	
Border STATES (25 populations)					972
<i>saccharum</i>					197
144*	AR	Benton	Gateway	35	
145*	AR	Crawford	Chester	44	
			Kimes Mountains		
154*	MO	Camden	Tunnel Dam	55	
179	AR	Polk	Rich Mountain No. 1	38	
180	OK	McCurtain	Idabell	25	
			Little River		
<i>schneckii</i>					120
90*	MO	Christain	Highlandville	25	
91*	MO	Texas	Clear Spring	21	
93*	MO	Pulaski	Big Pines River	15	
137*	MO	Taney	Hollister	28	
			Lake Taneycomo		
138*	MO	Texas	Jacks Fork River	31	
<i>floridanum</i>					253
121*	AR	Scott	Boles	44	
			Big Forche River		
122*	AR	Benton	Rogers	43	
			Devil's Eyebrow		
124*	AR	Crawford	Chester	43	
			Sugar Camp		
128*	AR	Carroll	Eureka Springs	43	
			King's Springs		
135*	AR	Carroll	Eureka Springs	43	
136*	AR	Polk	Rich Mountain No. 2	37	

*Population samples from previous studies

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO.†	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
intermediate					402
101*	IL	Effingham	Hill	46	
102*	MO	Lewis	Canton	26	
103*	IL	Lee	Dixon	46	
104*	IL	Ogle	Byron	48	
105*	IL	Henry	Cambridge	45	
132*	MI	Kalamazoo	Schoolcraft Nesbit Corners	50	
133*	MO	Dent	Montauk S.P.	52	
134*	MO	Morgan	Gravois Mills Gravois Springs	56	
142*	MO	Callaway	New Bloomfield Hiller Creek	33	
EXAMPLARS (30 populations)					1173
<i>grandidentatum</i> (UT)					254
28	UT	Utah	Alpine Fort Canyon	49	
48	UT	Wasatch	Deer Creek Reservoir Hanks Canyon	58	
51	UT	Utah	Timpagnogos Campground American Fork Canyon	51	
55	UT	Wasatch	Midway Snake Creek Canyon	50	
68	UT	Cache	Mendon Maple Bench	46	
<i>saccharum</i> (SAC 1, pure border states)					181
84*	IL	Tazewell	Peoria	50	
146*	IA	Jones	Wapsipinicon S.P.	21	
149*	MN	Scott	Spring Lake	23	
150*	MN	Benton	Foley	45	
153*	MO	Marion	Hannibal MarkTwain Cave	42	
<i>saccharum</i> (SAC 2, pure miscellaneous eastern)					237
79	WV	Grant	Mount Storm Edgewood Farm	47	
156*	MA	Worcester	Petersham	60	
165	OH	Geauga	Chardon Bass Lake Sugar Camp	46	
166	WV	Preston	Cranesville Fenston Farm	60	
167	OH	Medina	Cleveland M.P.S. Hinkley Ridge	24	

APPENDIX—POPULATIONS EMPLOYED IN ANALYSIS (continued)

POPULATION NO. 1	LOCATION STATE	COUNTY	LOCALITY	LEAVES IN SAMPLE	TOTAL LEAVES
<i>nigrum</i> (NIG)					111
82*	IA	Lee	Montrose	31	
85*	IA	Kossuth	Algona	50	
86*	IA	Kossuth	Algona	30	
<i>schneckii</i> (SCH)					197
87*	IL	Monroe	Fountain Gap	60	
88*	MO	Franklin	Fiddle Creek	45	
95*	MO	St. Francis	Koester	27	
96*	MO	St. Lewis	Eureka	42	
			Rankin Estate		
139*	MO	Franklin	Robertsville	23	
			Meramec River		
<i>floridanum</i> (FL 1, Crowley's Ridge)					159
123*	AR	St. Francis	Forest City	44	
125*	AR	Phillips	Helena	29	
126*	AR	Green	Paragould	43	
127*	AR	Phillips	Helena	43	
<i>floridanum</i> (FL 2)					34
106*	GA	Bartow	Emerson	12	
107*	GA	Cobb	Bolton	16	
108*	GA	Clarke	Whitehall	6	

TOTAL LEAVES IN STUDY

3408

NOTES: FIELD COLLECTION SITE LOCATIONS AND RAW DATA MEASUREMENT AVAILABILITY FOR ALL POPULATION SAMPLE SPECIMENS COLLECTED FOR THIS AND ALL OTHER STUDIES (ALL SPECIMENS CURRENTLY HOUSED AT LAVAL UNIVERSITY, QUEBEC, CANADA) Complete location information regarding collection sites and tables of all measurement data for this and all previous projects are available as follows. Portions of the senior author's field log are also available by direct request.

1. ADI Auxiliary Publications Project

Photoduplicating Service, Library of Congress, Washington, D.C. 20540.

ADI Document No. 3577 "Dynamics of Leaf Variation in Sugar Maples". Pooled collections from previous studies (Desmarais, 1952). Microfilm \$7.23. Photocopies \$21.30.

2. Microfiche Publications.

A. See NAPS Document No. 03410 for 520 pages of supplementary material. "Relationships of West Central Oklahoma Sugar Maples to Eastern and Western Species". Dent collections (1963-68) plus populations selected from Desmarais' pooled collections.

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A NOTE ON THE GROWTH HABIT OF FRINGED POLYGALA

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ABSTRACT

The green leaves and flowers of *Polygala paucifolia* occur along the terminal, upright portions of long thin rhizomes that grow out from a small perennial tuber. Each tuber sends out several new rhizomes annually. New tubers are produced at the scale leaf nodes of the horizontal portion of the rhizome through the multiplication of lateral buds and through secondary vascular growth. This mode of vegetative reproduction increases the longevity of a plant and spreads an individual laterally.

In this paper I describe the vegetative growth of *Polygala paucifolia* Willd. (Polygalaceae) emphasizing the development of the perennial, subterranean organs. Although these small tuberous structures are often included in herbarium material of *P. paucifolia*, a description of their ontogeny and role in the life history of the species is absent from systematic treatments of the genus (Wheeler, 1891; Miller, 1971).

There is little recent literature on the morphology and anatomy of the genus. Holm (1929) mentions the existence of what he inappropriately calls a "pseudo-rhizome", but he was unaware of its curious development. The following account is based on material excavated on several occasions during 1982 from natural populations growing in Harvard Forest, Petersham, Massachusetts, and from an oak woods near Bellows Falls, Vermont. I confirmed certain phenological observations by making repeat visits to marked plants. A survey of the herbaria of Harvard University and the New England Botanical Club failed to show any significant geographic variation in growth habit.

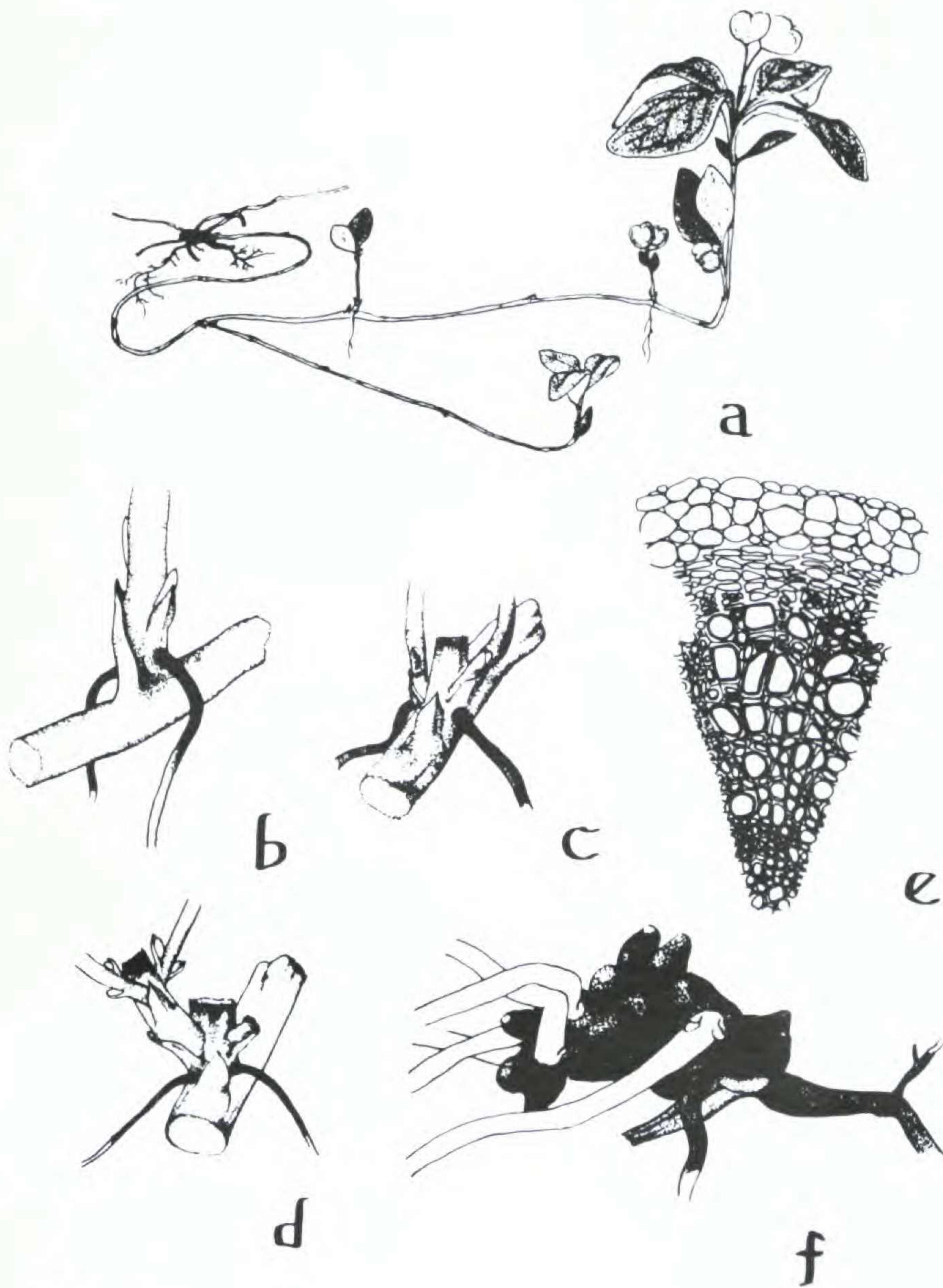
Polygala paucifolia blooms in Massachusetts during the latter part of May and the first two weeks of June, often forming conspicuous patches on the forest floor. A short vegetative axis, usually with basal cleistogamous flowers, supports 3-7 photosynthetic leaves and frequently terminates with a pair of chasmogamous flowers. Careful excavation reveals that this upright shoot is the end of a pale, thin (1.0-1.5 mm diameter) horizontal stem, resting 1-2 cm beneath the soil litter. This stem can be traced back 5-30 cm to a small (1-5 mm diameter), well rooted, tuberous organ from which several other horizontal stems radiate.

Along this horizontal stem occur scale leaves arranged in a spiral fashion, with internodes ranging from one to seven centimeters. Each scale leaf subtends an axillary bud that may be in one of four conditions: (1) inactive, (2) growing as a horizontal shoot, the parent axis then being branched, (3) growing as a short vertical vegetative shoot, (4) growing as a short vertical shoot terminating in a pair of cleistogamous flowers. Typically, the cleistogamous flowers are found on a lateral appendage near the base of the chasmogamous flowering stem. All four conditions are represented in Figure 1a.

A tuber is the source of the horizontal stems, but the critical feature of the growth habit is that the horizontal stems are a source of new tubers. These tubers develop at the scale leaf nodes over the course of several years, and three processes are involved: root initiation, meristem proliferation, and secondary vascular growth. The following account describes a typical course of tuber development.

When a lateral bud grows out, one or two adventitious roots are initiated on the new stem immediately adjacent to the parent axis (Fig. 1b). There are no roots on the parent stem and no further roots will form at this node. Immediately above the adventitious roots, a pair of scale leaves and axillary buds are initiated, followed by a long internode separating them from subsequently formed photosynthetic leaves. The lateral shoot that bears these structures will live through the summer, fall, and possibly winter before dying back to a point just above the scale leaves. The buds in the axils of those scale leaves then grow out, and each in turn will form its own pair of basal scale leaves and axillary buds (Fig. 1c). Note that the plane of bud insertion is always perpendicular to that of the previous year. This process of shoot die back and basal bud proliferation is repeated annually and leads to a tuber (at this stage, really a condense sympodial branch system) with an increasing number of meristems (Fig. 1d). About the third year in its development, the tuber becomes independent of the parent axis which decays at the adjacent internodes. Continued meristem proliferation and secondary vascular growth in both roots and stems (Fig. 1e) leads to a mature tuber (Fig. 1f).

The tuber contributes toward the longevity of the individual by its own survival and through the potential it provides for the development of new tubers on the annual crop of runners. This growth



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Figure 1. *Polygala paucifolia*: Early stages of tuber development. **a.** Habit sketch, 1/3 X. **b.** First year; two roots and two basal buds are initiated. **c.** Second year; basal buds grow out initiating their own basal buds. **d.** Third year; basal bud proliferation continues, but here illustrated for only one branch and the buds slightly separated. **e.** Root, transverse section, 100 X. **f.** Habit sketch of mature tuber, 3X.